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Comparison of Northern and Southern Populations of *Epitonium tinctum* (Carpenter, 1864) on the California Coast

by

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Abstract. *Epitonium tinctum* (Carpenter, 1864) was collected for several years from Bodega Head to the north and from Carpinteria Beach to the south of Point Conception, California. Northern populations contained longer shells than southern populations. Northern snails became sexually mature and changed sex at a larger size than southern snails. There were no distinguishable differences in the weight and width of specimens between northern and southern snails of similar length. Variation in shell shape (squat versus elongate) between populations did not exceed variation within each population. Shell length and the number of body whorls overlapped substantially between the two sites. The size and abundance of snails collected monthly fluctuated more throughout the year in the northern population than in the southern population.

INTRODUCTION

ALONG THE WEST coast of North America the wentletrap *Epitonium* (=*Nitidiscala*) *tinctum* is found intertidally in association with the aggregate or clonal anemone *Anthopleura elegantissima* (Brandt, 1835). *Epitonium tinctum* ranges from Magdalena Bay, Baja California to Forrester Island, Alaska (DUSHANE, 1979). As protandric hermaphrodites, the snails mature first as males; then, at a larger size they change sex and function as females (BULNHEIM, 1968; BREYER, 1982). Females produce a number of sand-encrusted egg cases which are strung together with a strong elastic mucous thread attached to the substrate or to the shell. When exposed at low tide, snails bury themselves in the sand between anemones and are often aggregated around a cluster of egg cases. When submerged during high-tide periods the snails become active and feed on the expanded tentacles of the anemones (HOCHBERG, 1971; SMITH, 1977; BREYER, 1982). In order to feed, the snails evert an acrembolic proboscis and either slip the distal end over a tentacle tip or attach it at some point along the length of the tentacle. Jaws and radula are used to sever a portion of the tentacle which is then ingested upon retraction of the proboscis (RESCH, 1972).

The shell of *Epitonium tinctum* can grow to over 10 mm in length. It has three nuclear whorls and up to 8 postnuclear whorls with about 12 thin axial costae continuous from whorl to whorl. STRONG (1941) examined shells from north and south of Point Conception, California, and noted that northern specimens were longer and appeared to be heavier and broader than southern individuals. He suggested the subspecific name of *subcoronatum* for the northern form. Although DUSHANE (1979) described similar differences, she did not recognize the subspecies *subcoronatum* because radulae from northern and southern snails were indistinguishable.

Individuals of populations living in food-rich environments or in warm climates may be expected to grow faster than those living in more severe environments. This faster

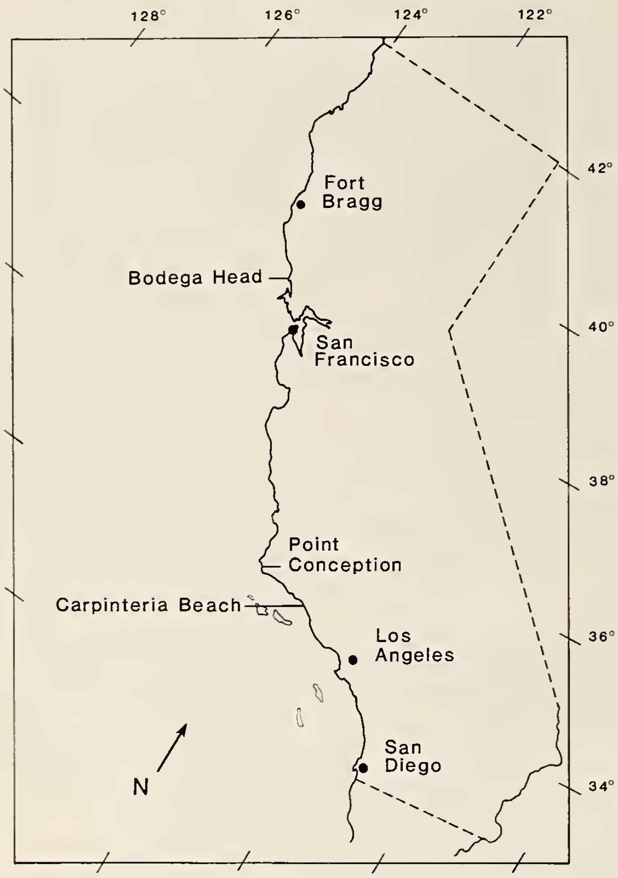

Figure 1

Map of California showing two study sites located north (Bodega Head) and south (Carpinteria Beach) of Point Conception.

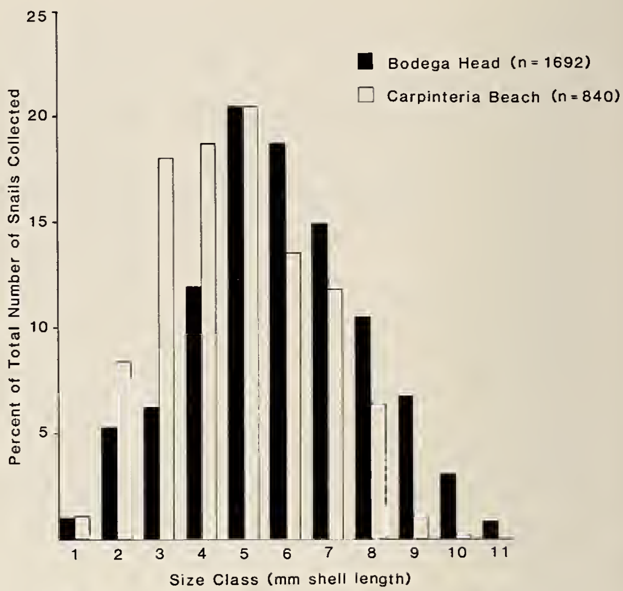

Figure 2

Comparison of *E. tinctum* shell length and the percentage of total number of snails collected from 1977 to 1980.

growth may lead to an altered size at maturity and perhaps an important difference in generation time. In the present work we document differences within and between populations of *Epitonium tinctum* to the north (Bodega Head) and to the south (Carpinteria Beach) of Point Conception, California (Figure 1). Providing the major basis for comparison are shell parameters, which include: length, width, weight, and number of whorls and costae. Distinct population modes were computed from measurements of shell length. The mean minimum size at onset of sexual maturity and sex change were calculated from lengths of juveniles, males, and females. Additionally, fluctuations in size and abundance were noted monthly from July, 1977, to July, 1979, for populations at Bodega Head, and from July, 1978, to June, 1980, for populations at Carpinteria Beach.

MATERIALS AND METHODS

Collection Sites

The northern collecting site was in Horseshoe Cove located on the exposed outer coast of Bodega Head, Sonoma County, California. In a protected area on the northern side of the cove, a 3-m-wide surge channel located about 10 m from shore is bordered on one side by a cliff. The channel is parallel to the cliff for about 15 m until its mouth opens toward the west. Wave disturbance in this channel is reduced, not only because waves break to the south, but also because it is protected by an extensive rock shelf. At this site clones of *Anthopleura elegantissima* cover extensive areas on the sides and bottom of the channel. In the summer and fall, when wave action is reduced, the sand between the anemones is fine grained and at least 10 mm deep. During the winter, when wave action is heaviest, the amount of fine sand between the anemones is reduced, disappears altogether, or is replaced by coarser sand. Snails were collected from the anemone beds on both sides of the channel.

The rocky reef area at Carpinteria Beach State Park, Santa Barbara County, California was the southern collecting site. Carpinteria Beach, like much of the southern California coastline south of Point Conception, is characterized by sandy beaches interrupted by intermittent rocky outcrops or headlands. The Carpinteria Beach site consists of a sandy beach extending out from the cliff about 100 m to where the first rock outcrop begins. In the mid-intertidal region of the rocky reef both clonal and solitary *Anthopleura elegantissima* are present. *Epitonium tinctum* is most often found in protected areas on these rocks in sand which accumulates within pockets between clonal anemones and beneath the algal cover of *Ulva lobata* (Kutzing, 1849) and *Gigartina canaliculata* (Harvey, 1841).

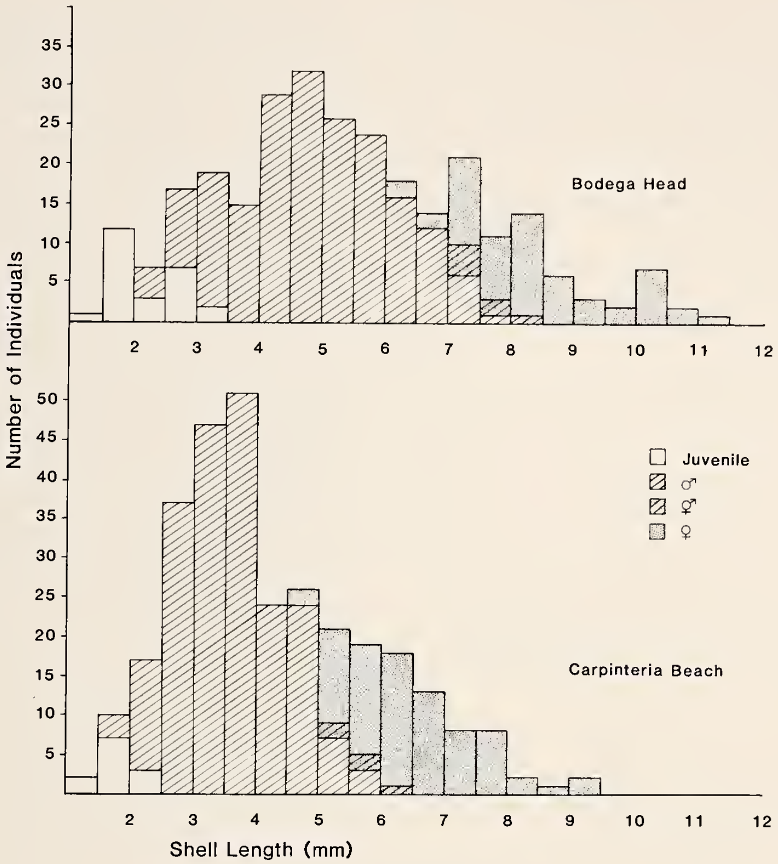

Figure 3

Comparison of *E. tinctum* shell length versus the number of juveniles, males, and females in each population. Snails in transition from male to female (possessing both spermatozeugmata and ova) are also indicated.

Although this area receives gentle surf year around, a perceptible change occurs in the structure of the beach between summer and winter. In summer, a sand bar fills in the area between the shore and the first rock outcrop. Sand, several centimeters in depth, fills in the crevices between clonal anemones and covers many of the solitary anemones, which are primarily located lower in the intertidal. Algae flourish during this time and cover extensive surfaces of rocks. During winter storms much of the sand cover is removed from between the clonal anemones and the algal cover on the rocks is reduced.

Methods

Epitonium tinctum was collected approximately monthly at low tide from each site; from July, 1977, to June, 1979, at Bodega Head and from July, 1978, to June, 1980, at Carpinteria Beach. Additional collections were made in 1980 and 1981 at both locations. Snails were collected by carefully searching among aggregations of *Anthopleura elegantissima* in an area approximately 3 m^2 for 30 minutes. Similar areas, exposed at mean lower low water, were used for repeated collections at each site. Snails were located by visually scanning the area or by lightly stroking the anemones with fingertips. Pressure on the anemone body caused the release of a small amount of fluid which washed over the anemone bed and removed some sand and debris. When the tip of a snail or a clump of eggs was spotted it was carefully removed by hand. Often a mucoid thread was attached from the snail or eggs being removed to other snails and eggs in an aggregation. Care was taken to remove all snails and eggs in a particular aggregation before searching for additional snails.

Lengths and widths of snails were measured using a variety of dissecting microscopes with calibrated ocular micrometers. The number of post-nuclear whorls was determined by placing the shell with the operculum facing upward and counting from the largest body whorl to the smooth nuclear whorls. Axial costae were counted from the first costa behind the outer lip, around the body whorl,

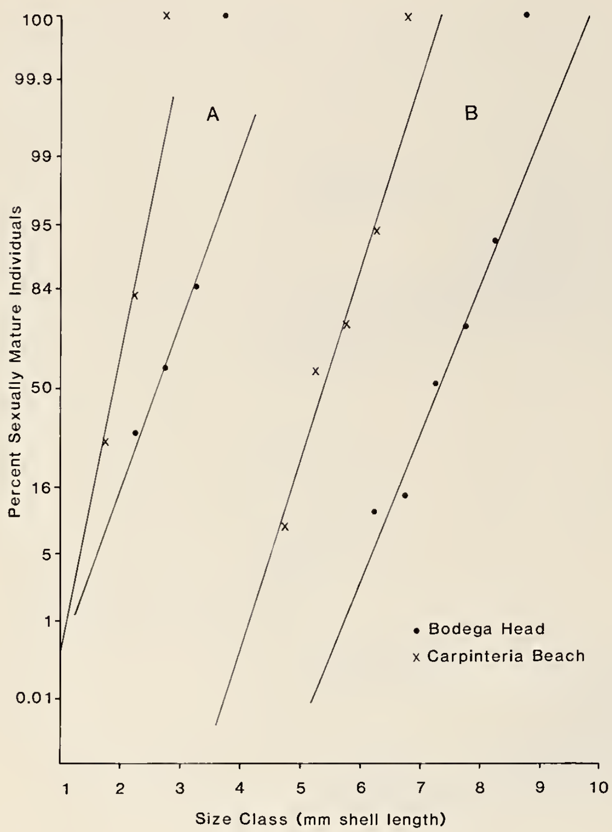

Figure 4

Mean minimum size of *E. tinctum* at onset of sexual maturity. A. Males replaced juvenile snails at an average length of 2.6 mm in Bodega Head and 1.9 mm in Carpinteria Beach. B. Females replaced males at an average shell length of 7.3 mm in Bodega Head and 5.4 mm in Carpinteria Beach. No significance test was run between sets of lines; an appropriate test is not yet in print (Wenner, in preparation).

to the point where the first costa met the costa directly above it. Weights (to 0.1 mg) were obtained on a Mettler balance from animals and shells originally preserved in 50% isopropyl alcohol, which were removed from the alcohol and allowed to air dry 24 hours at room temperature before weighing.

To determine sex, snails preserved in 70% ETOH or 50% isopropyl alcohol were first measured and then placed in a vial filled with Bouin's solution for 24 hours to dissolve their shells. Individuals were then examined with a dissecting microscope at approximately 50×. Males were recognized by the presence of spermatozeugmata, which were clearly visible as very white, almost iridescent strands densely packed in the gonad especially to the right of the stomach. Females were distinguished by the absence of spermatozeugmata and the presence of oocytes and ova. Several snails, termed hermaphroditic, were characterized by having proximally located spermatozeugmata and distally located oocytes and ova in their gonads.

Probability Paper Analysis of Polymodal Frequency Distributions

The technique of plotting cumulative normal distributions on probability graph paper, first descrbed by HARDING (1949), with methodology presented by CASSIE (1950), is a valuable graphical method with which to analyze bimodal or polymodal size-frequency distributions in a population. In a polymodal size-frequency sample, individual modes may be expanded and the mean and standard deviation calculated from each mode (see CASSIE, 1954, for method). If modes are compared from two or more populations, subtle differences may be distinguished. Probability paper analysis has been utilized to compare sex ratios and size in crustacean populations (WENNER, 1972) and to define and compare the mean minimum size at onset of sexual maturity in populations of the sand crab *Emerita analoga* (Stimpson, 1857) from different locations (WENNER *et al.*, 1974).

RESULTS

A compilation of size-frequency data for all snails collected and measured over a two-year period in Bodega Head and Carpinteria Beach is presented in a histogram (Figure 2). From these data a polymodal analysis of each population was calculated by the use of probability graph paper. That analysis indicated larger snails were more prevalent at the northern site than at the southern site. The modes that appear in each population were then expanded, also by the use of probability paper. Three distinct modes were calculated for each population consisting of small, medium, and large snails. For Bodega Head these values were, respectively, as follows: $\bar{x} = 2.20 \pm 0.55$ mm, n = 152; $\bar{x} = 5.40 \pm 1.20$ mm, n = 1134; $\bar{x} = 8.35 \pm 1.15$ mm, n = 406. For Carpinteria Beach values were, respectively: $\bar{x} = 2.65 \pm 0.77$ mm, n = 193; $\bar{x} = 4.75 \pm 0.90$ mm, n = 487; $\bar{x} = 7.20 \pm 0.90$ mm, n = 160. Since these snails are protandric hermaphrodites, changing from juveniles to males and then from males to females as they grow, the modes that appear possibly represent the juveniles, males, and females in each population.

More than 600 snails were examined for the presence or absence of spermatozeugmata during spring and fall (Figure 3). The size at which these protandric hermaphrodites became sexually mature and changed sex was greater in the northern population than in the southern population. In the transition from male to female in each population, snails were occasionally found with both spermatozeugmata and ova present. The data for transition of juveniles to males and males to females were plotted on probability paper (Figure 4) and the mean minimum size was calculated (*e.g.*, WENNER *et al.*, 1974). The mean size of females was larger at Bodega Head (7.3 mm) than at

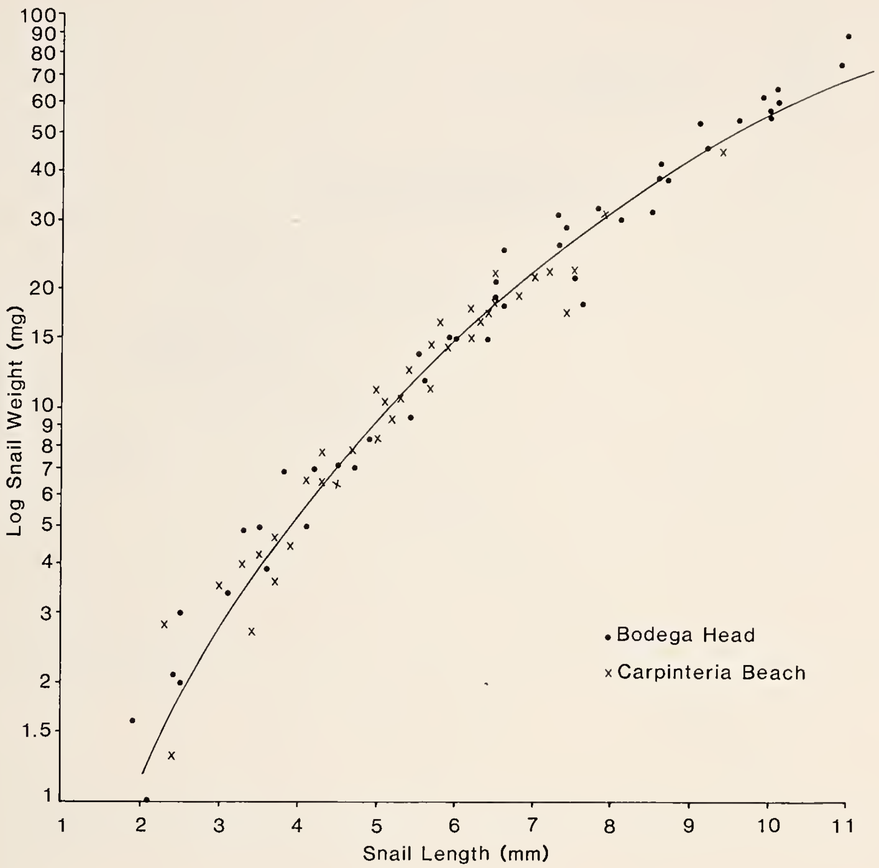

Figure 5

Comparison of *E. tinctum* length versus weight. A complete overlap existed between sets of points, so only one curve was fitted (by inspection).

Carpinteria Beach (5.4 mm). The mean size of juveniles was also larger at Bodega Head (2.6 mm) than at Carpinteria Beach (1.9 mm).

The weights of snails (from 1.7 to 91.3 mg) in each population were obtained for snails ranging in length from 1.9 to 11.0 mm (Figure 5). The results revealed little variation in weight of snails at the same length between populations. The width of snails relative to shell length from both populations varied somewhat (Figure 6). We observed that some snails within each population appeared to have either a more squat or more elongate shell shape than the others. Although the range of variation within each population was notable, regression lines did not differ significantly between northern and southern populations. Snails of similar lengths varied considerably in number of body whorls (Figure 7), but did not differ appreciably between populations. The number of axial costae on the largest body whorl of shells from both locations ranged between 11 and 14, which agreed with DuShane's (1979) findings.

The size and abundance (Figure 8) of *Epitonium tinctum* collected monthly at Bodega Head fluctuated more than in similar collections from Carpinteria Beach. Small snails (less than 3 mm) were found occasionally throughout the year at Bodega Head; however, they were most common from late winter to early summer. In 1978 many small snails were found in March and April; in 1979 few small snails were found until June; in 1980 many small snails were found in January. Every year during the summer and early fall, snails were common. In 1978 the mean shell length increased every month during this period. In the fall large females (longer than 8 mm) were most common, and particularly large clusters of egg cases associated with large aggregations of snails were found (Figure 9A). In the late fall and early winter the abundance of snails declined. Snail abundance decreased from December, 1977, to February, 1978, and from February to May, 1979. Snails remained rare until an influx of small snails appeared.

No clear annual pattern was shown at Carpinteria

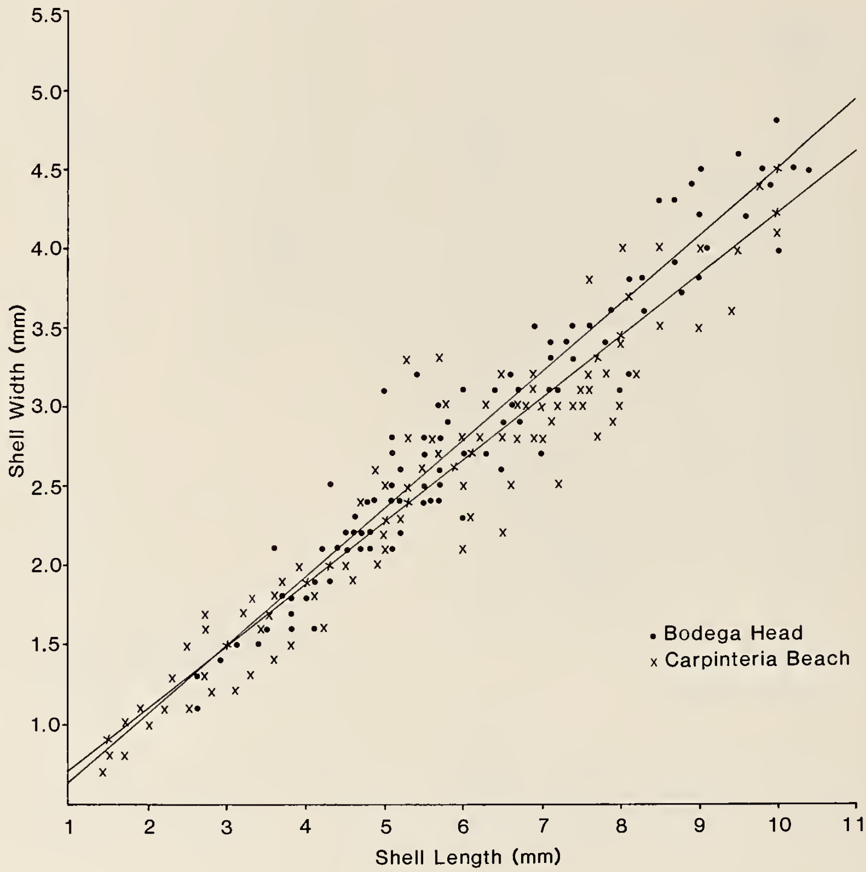

Figure 6

Comparison of *E. tinctum* length versus width. The slopes of the lines were not significantly different (P > 0.01). The regression for Bodega Head was y = 0.22 + 0.43x (n = 95) and Carpinteria Beach was y = 0.33 + 0.39x (n = 94).

Beach for size or abundance of snails collected from July, 1978, to June, 1980. The mean snail length (4.5 to 6.0 mm) remained fairly constant through time. Newly settled snails (less than 3 mm in length) occurred commonly at all seasons. The largest individuals were observed sporadically throughout the year. Egg masses were recorded in the field in all collections in equal abundance. Snails with eggs most commonly occurred as individuals or in small groups (2–4 individuals) with few egg capsules per egg mass (less than 50 to about 500). Larger snail groups (10–15 individuals) and large egg masses (1000–5000 eggs) occurred without respect to season (Figure 9B). During the winter of 1981, severe storms washed away large amounts of sand from Carpinteria beaches. It was difficult to cross on foot from the cliff to the first rock outcrop, because of the diminished sand coupled with large waves. In February, 1981, the population of snails was greatly reduced. An influx of small snails (mean length 3.5 mm) was noticed in the spring (April, 1981). A population fluctuation occurred at Carpinteria Beach that year similar to fluctuations observed at the Bodega Head site.

DISCUSSION

Our results support the literature on physiological variation in intertidal molluscs summarized by NEWELL (1964). He concluded that northern species generally attain a larger final size than southern ones. WEYMOUTH *et al.* (1931) studied the razor clam *Siliqua patula* (Dixon, 1789), and concluded that growth in southern localities was initially more rapid, but less sustained and hence led to smaller total lengths. There are several reasons why snails may grow larger at higher latitudes. Higher latitudes generally imply a decrease in temperature coupled with an increase in environmental stresses. CHOW (1975) concluded that the largest *Littorina scutulata* (Gould, 1849) had

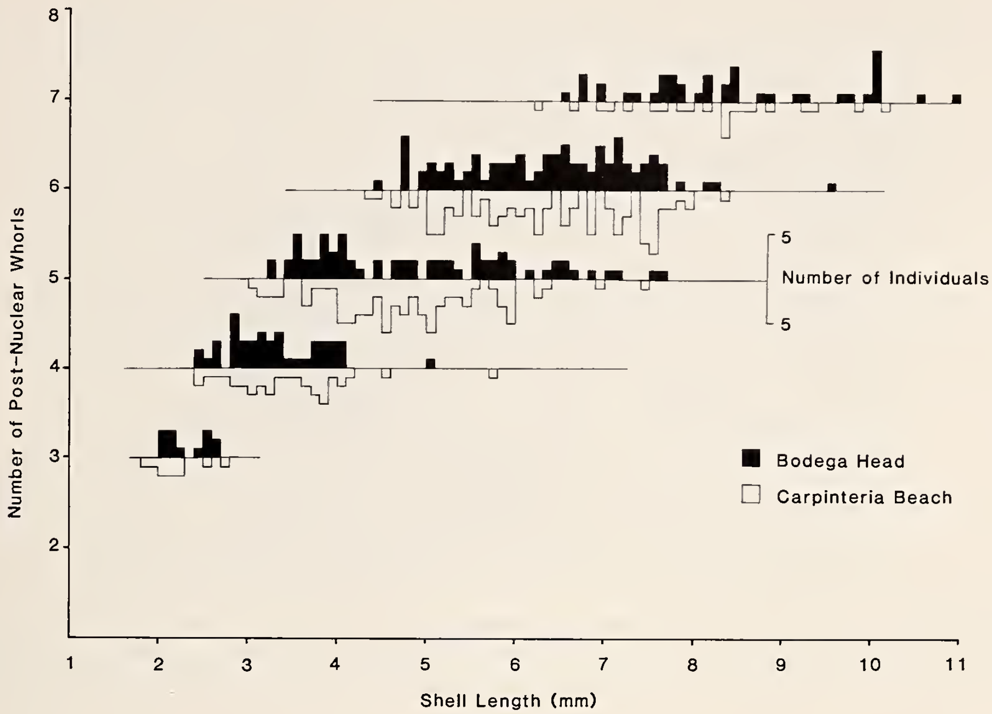

Figure 7

Comparison of *E. tinctum* shell length and number of post-nuclear whorls. Along each line the numbers of individuals are arranged by collecting locality.

higher tolerances to desiccation, wave shock, and osmotic stress. Thus, a larger snail may be equipped to survive the harsher environment of higher latitudes better than a smaller snail.

Recently Breyer (personal observation) observed that southern California *Epitonium tinctum,* collected from Santa Barbara and raised in the laboratory at the University of California, Santa Barbara, are capable of growing as large as northern California snails. At present we do not know why snails in the field in southern California do not grow as large as those collected in northern California.

Latitudinal variations in populations of *Epitonium tinctum* closely resemble those found by FRANK (1975) for the black turban, *Tegula funebralis* (A. Adams, 1855). In addition to finding larger snails in northern latitudes, Frank found that individuals in northern *Tegula* populations mature at a larger size and have irregular recruitment.

ROBERTSON (1981) reported similar size differences between populations of *Epitonium albidum* (Orbigny, 1842) in the British Virgin Islands and Barbados. The largest Virgin Island males were 8 mm long and females ranged to 16 mm. The largest Barbados Island males were 6 mm long while females reached 14 mm although most were 11 mm or less in length.

The northern California population of *Epitonium tinctum* fluctuated in size and abundance more than the southern California population and had a definite periodicity. In winter, snail populations declined markedly in the north. Severe winters are known to cause increased mortality in intertidal molluscs unless animals can migrate or are passively washed to deeper waters, or unless they can escape into crevices to hide (CRISP, 1964). *Epitonium tinctum* was difficult to locate among anemones during winter. It was assumed that most snails were washed off the rocks and died, but others may have escaped and lived out the winter in protected areas. Even if adults do survive the winter months, there is evidence that they may not increase in size appreciably until the spring. *Thais* (=*Nucella*) *lapillus* (Linné, 1758) grows little from October to March (LARGEN, 1967), and shell growth in *Tegula funebralis* ceases completely from November to February (FRANK, 1975). The return of spring signifies a period of larval settlement and the cycle continues. Snails grow during summer and fall until the onset of winter storms. Southern California, in contrast to the north, generally has milder winters, calmer waters, and warmer temperatures. In the southern area it is common to see all stages in the life cycle of a snail throughout the year.

In the north, *Epitonium tinctum* larvae may survive in

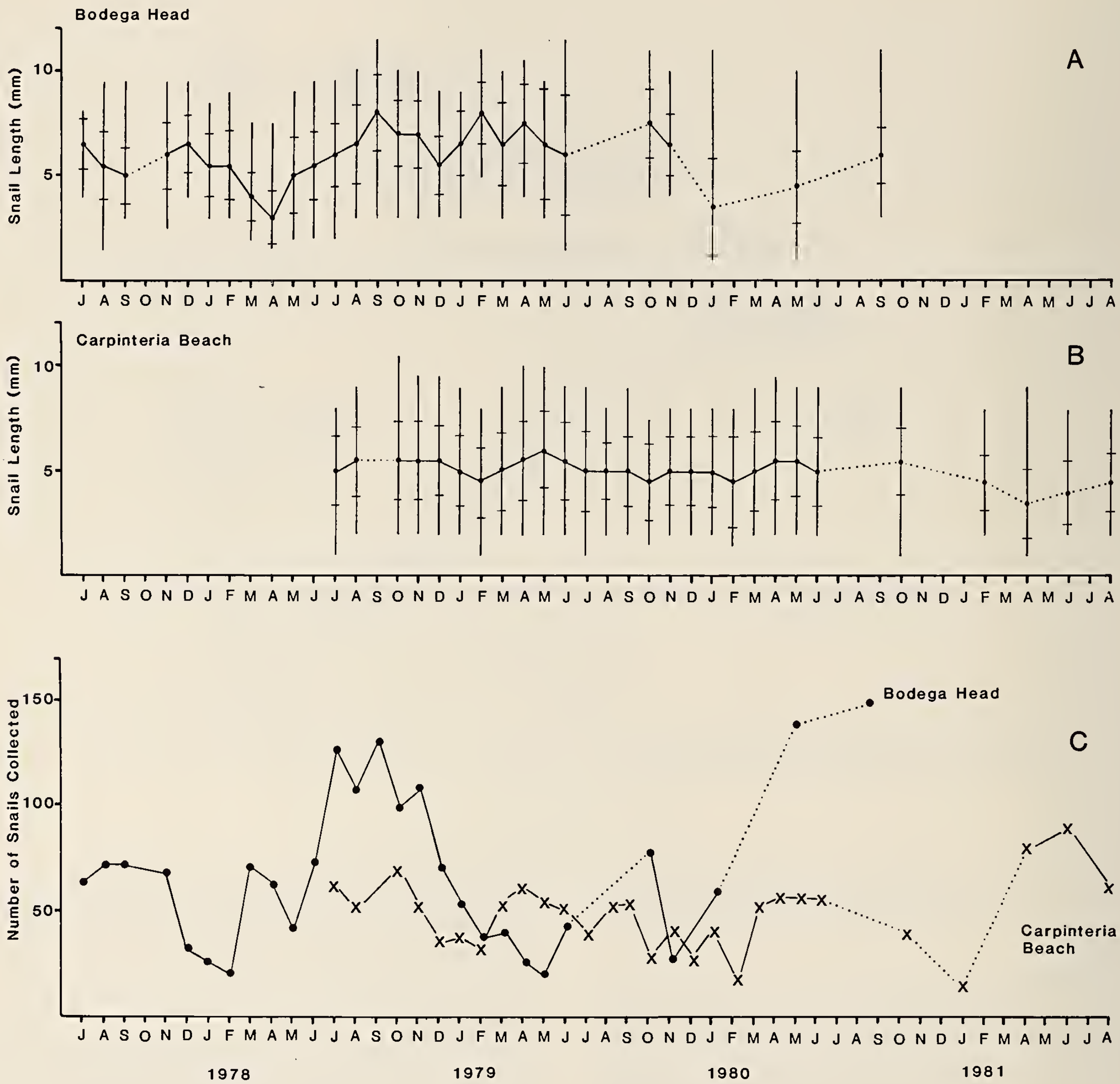

Figure 8

Size (including mean and standard deviation) and abundance of snails collected at Bodega Head and Carpinteria Beach from June, 1977, to July, 1981. A. Bodega Head, size. B. Carpinteria Beach, size. C. Bodega Head and Carpinteria Beach, abundance.

the plankton from late September until settlement, which often occurs as late as June. In the south, young snails and eggs are found throughout the year. Preliminary observations indicate the larvae of *E. tinctum* grow considerably before they undergo metamorphosis. Before hatching, veligers of *E. tinctum* measure about 70 μm in length. In the laboratory we have kept them alive for more than two months, at which time they had attained a size of more than 250 μm but had not yet metamorphosed. In the field the smallest snail observed during more than two years of study was 1.1 mm; apparently, veligers grow considerably in the plankton before they settle. DEHNEL (1955) looked at growth rates of embryos and larvae of northern and southern gastropod populations. He concluded that the rates of growth of embryos and larvae in northern gastropod populations are often 2 to 9 times greater than in southern populations of the same species at a given temperature.

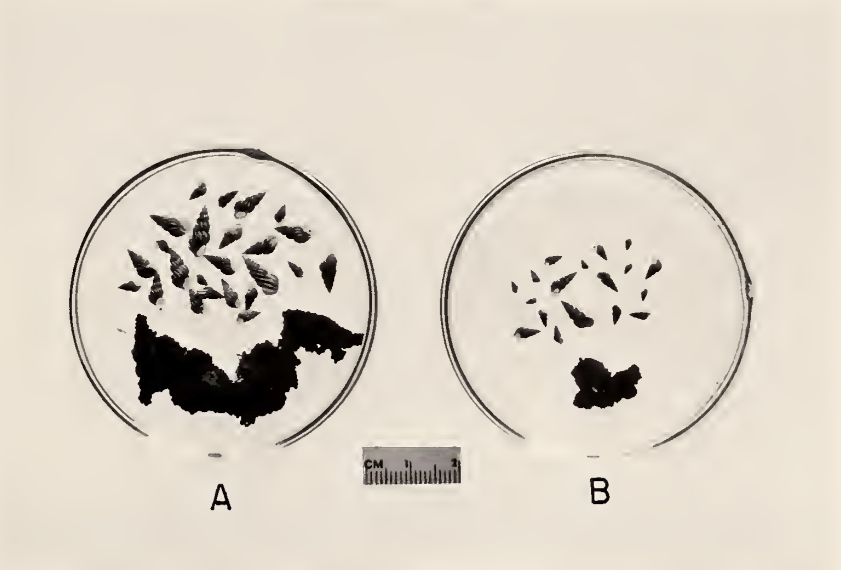

Figure 9

Comparison of the largest groups of snails and their associated egg masses found in fall 1980 collections. A. Bodega Head (26 September 1980; SBMNH 33878). B. Carpinteria Beach (23 October 1980; SBMNH 33879).

Once veligers metamorphose, growth in general is faster in warm than in cold seas, but this does not necessarily mean the largest species live in warm seas. The largest snails may be the slow-growing species found in cold water; and within a species, an individual is likely to grow more slowly, but become larger and older, at the northern limits of its distribution (Frank, 1969). This theory is consistent with our observations. Larger *Epitonium tinctum* were found north of Bodega Bay in Fort Bragg, and the largest specimens were recorded from Forrester Island, Alaska, the northern limit of distribution for this species.

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